

## Dynamic Pattern Formation Leads to $1/f$ Noise in Neural Populations

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We present a generic model that generates long-range (power-law) temporal correlations,  $1/f$  noise, and fractal signals in the activity of neural populations. The model consists of a two-dimensional sheet of pulse coupled nonlinear oscillators (neurons) driven by spatially and temporally uncorrelated external noise. The system spontaneously breaks the translational symmetry, generating a metastable quasihexagonal pattern of high activity clusters. Fluctuations in the spatial pattern cause these clusters to diffuse. The macroscopic dynamics (diffusion of clusters) translate into  $1/f$  power spectra and fractal (power-law) pulse distributions on the microscopic scale of a single unit.

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Long-range temporal correlations occur in many physical systems, leading to power spectra that behave as  $1/f^\alpha$ , where  $\alpha$  is an exponent close to unity. Such power spectra, generally labeled  $1/f$  noise, are the characteristic signature of fluctuations on many time scales [1]. In particular,  $1/f$  noise has been observed in the pulse trains of nerve cells belonging to various brain structures, such as the auditory nerve [2] and the mesencephalic reticular formation [3]. The reported exponents, which depend both on the presence or absence of a sensory stimulus [2] and on the state of the animal (REM sleep vs awake state) [3], vary from 0.68 to 1.13. The power-law behavior for spike train power spectra lies within the range 0.01 to 10 Hz, extending typically over 1–2 decades.

We propose here a novel mechanism for generating  $1/f$  noise that replicates the correlational structure of neural signals in a network model with pulselike interactions. Strong correlations are induced in the model by spontaneous symmetry breaking of the spatial pattern of activity across the network. This pattern is, however, *metastable* in the presence of noise: clusters of high activity diffuse throughout the system while undergoing strong internal fluctuations. The spatial pattern's *persistent* dynamics result in fractal (power-law) interevent interval distributions and  $1/f$  noise in the temporal dynamics of single units.

The model consists of a cyclic  $100 \times 100$  lattice of units characterized by a voltage variable  $V_i$ . Each unit models a nerve cell as a simple RC circuit ( $\tau = 20$  msec) with the addition of a reset mechanism. Once a unit reaches a threshold voltage  $V_{th}$ , it emits a pulse that is transmitted in one iteration (1 msec) to connected neighboring units, and the potential is reset by subtracting the voltage threshold:

$$V_i(t+1) = \begin{cases} e^{-1/\tau} V_i(t) + I_i(t), & V_i(t) < V_{th}, \\ V_i(t) - V_{th}, & V_i(t) > V_{th}, \end{cases} \quad (1)$$

where the current  $I_i(t) = \sum_j W_{ij}^E \Theta[V_j(t) - V_{th}] - \sum_j W_{ij}^I \Theta[V_j(t) - V_{th}] + I_i^{ext}$  represents the coupling of

the unit to excitatory (inhibitory) pulses of nearby units through the matrix  $W_{ij}^E$  ( $W_{ij}^I$ ) and to an independent external current. Such a model, known as an integrate-and-fire model [4], is similar to a recently studied self-organized criticality model for earthquakes [5]. The model's match to experimental neurophysiological data is described in detail elsewhere [6].

The pattern of local excitatory and inhibitory connections is *center surround*. Each unit is excitatorily connected to  $N = 50$  units chosen from a Gaussian probability distribution of  $\sigma = 2.5$  lattice constants, centered at the unit's position.  $N$  inhibitory connections per unit are chosen from a uniform probability distribution on a ring eight to nine lattice constants away. (A deterministic version of the center-surround scheme was also tested, which we shall refer to as isotropic connectivity.) The weight of the excitation and inhibition, in units of voltage threshold, is  $W^E = \alpha/N$  and  $W^I = \beta W^E$ . The external input is modeled independently for each cell as a Poisson process of excitatory pulses of magnitude  $1/N$ , arriving at a mean rate  $\lambda_{ext}$ .

Scaling the relative degree of inhibition  $\beta$  while keeping the sum of excitation and inhibition constant leads to a transition from a spatially homogeneous state to a clustered activity state. This transition can be understood using a mean-field description of the dynamics, where we write the pulse rate  $f_i$  as a function of the averaged currents  $I_i$ :  $f(I) = \{T_{ref} - \tau \ln[1 - 1/I\tau]\}^{-1}$  [7], where  $T_{ref}$  is the minimum dead time between pulses [8]. In this approximation, the dynamics associated with Eq. (1) simplify to

$$\frac{dI_i}{dt} = -I_i + \sum_j W_{ij} f(I_j) + I_i^{ext}. \quad (2)$$

The homogeneous solution  $I_i = \bar{I}$  for all  $i$  is stable only if the Fourier transform of  $W_{ij}$  satisfies  $\tilde{W}(k)f'(\bar{I}) - 1 < 0$  for the entire (discrete) set of  $k > 0$ . As one increases the relative strength of inhibition, clusters of

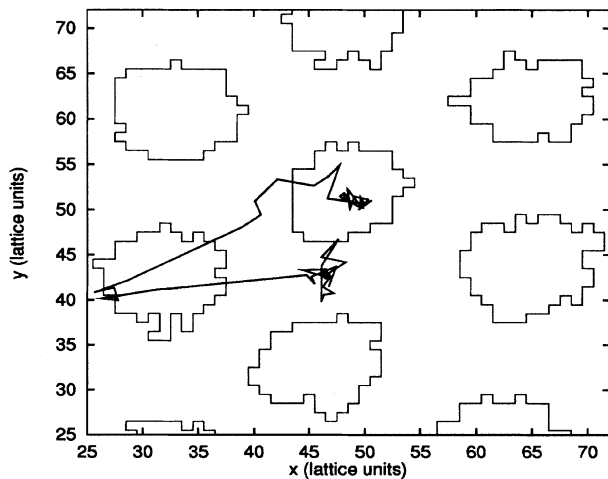


FIG. 1. The summed activity for the network over any 50 msec of simulation reveals a nearly hexagonal pattern of clusters of high activity. This roughly hexagonal pattern, however, does not remain fixed, since individual clusters undergo vibratory and diffusive motion and thus shift in position. To illustrate this, we superimpose onto the static snapshot of activity the motion of the center cluster through time (bold line). Each vertex of the bold line represents the cluster's position averaged over successive 50 msec intervals. For model parameters  $\alpha = 1.3$ ,  $\beta = 0.67$ , and  $\lambda = 2.3$  inputs per msec, the diffusion constant is  $0.2[\text{lattice units}]^2/\text{msec}$ .

high firing activity develop. The clusters form a hexagonal grid across the network, as illustrated in Fig. 1. The level of external input also influences the spatial pattern; for higher values of input the clusters merge into stripes. The transition from a homogeneous state to hexagonal clusters to stripes is generic to many nonequilibrium systems in fluid mechanics, nonlinear optics, reaction-diffusion systems, and biology [9–11]. In the mean-field description, the dynamics (2) are subject to a Lyapunov potential function [12,13] so that the system must relax to a stable state—persistent dynamics are ruled out.

However, the mean-field equations [14–16] do *not* capture the essential dynamics of pulse-coupled networks responsible for the spatial pattern's metastability. Partial synchronization inside local populations induce large fluctuations which destabilize the mean-field pattern. These fluctuations allow clusters of high activity to diffuse throughout the system, as can be seen from the cluster's trajectory in Fig. 1. Simulations performed with constant (instead of stochastic) input and with isotropic connectivity reveal that the system is intrinsically chaotic.

Since clusters diffuse, the instantaneous and long-time averaged patterns of activity can be strikingly different. Figure 2 displays the activity of the network with isotropic connections averaged over 100 000 msec for several values of external input. In all cases, the instantaneous pattern of activity is a hexagonal grid of high activity clusters. For low external input values, the highly fluid

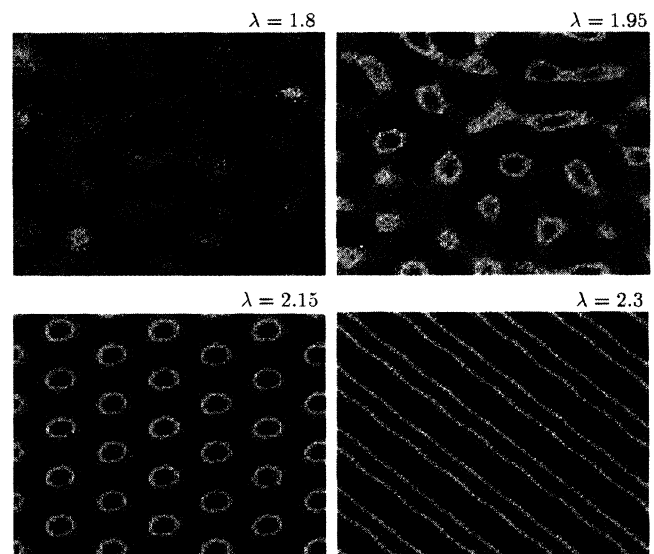


FIG. 2. Long-time average (100 000 iterations) of activity in a lattice of pulse-coupled units with symmetric center-surround connections. The system is ergodic only at low external input rates ( $\lambda = 1.8$  inputs/msec). At intermediate input levels ( $\lambda = 2.15$ ), spatial structures remain in the pattern even after more than 100 sec of simulation. For higher input ( $\lambda = 2.3$ ), the long-time average shows diagonal stripes as a result of one-dimensional motion of clusters.

motion of clusters restores the symmetry broken at the level of instantaneous states: the time-averaged activity patterns are uniform up to statistical fluctuations. Higher input “crystallizes” the hexagonal lattice of clusters by slowing diffusion; in analogy to atoms in a liquid-solid transition, clusters become constrained to vibrate around fixed sites. The system becomes nonergodic even at long timescales. The symmetry of the hexagonal lattice itself can be broken, leading to a preferred axis of cluster motion and the appearance of stripes in the time-averaged activity patterns, a precursor to the striped phase in the instantaneous pattern.

In the transitional regime between fluid and crystalline patterns, the slow diffusion of clusters cause fractal  $1/f$  signals in single unit pulse trains, as we shall now show. We focus on two quantities: The first is the interevent interval (IEI) distribution  $P(t)$ , and the second complementary quantity is the autocorrelation  $C(t)$  (or its Fourier transform, the power spectrum), which measures the number of events separated by time  $t$ .

The IEI distribution, shown in Fig. 3, decays as a power law in  $t$  with exponent  $\gamma = 1.7$ , over one decade (from 25 to 300 msec). The correlation  $C(t)$  (Fig. 4) decays slowly via a power law with exponent  $-0.21$ . At the upper temporal cutoff of 300 msec for the power law behavior, the correlation function reaches the baseline of chance coincidence. The correlation implies that the

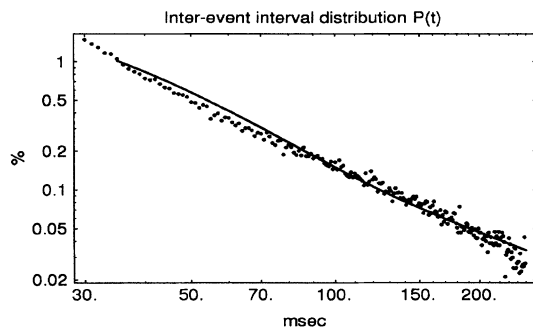


FIG. 3. The average interevent interval distribution for 19 cells. Superposition of exponential distributions from the cluster frame of reference (solid line) results in a power law  $P(t) \sim t^{-1.7}$  in the fixed unit frame.

power spectrum at low frequencies decays as  $1/f^{0.8}$ : the spectrum can thus be categorized as “ $1/f$ ”.

We gain an understanding of how a power law for  $P(t)$  arises by tracking a cluster of high activity as it diffuses through the system and measuring the IEI distribution for fixed distances relative to the cluster center. In the cluster frame of reference, activity rates do not change in time, so we expect to find a distribution function with a single characteristic time scale. Indeed, the measured distribution functions  $P_r(t)$  can be approximated closely by exponentials:  $P_r(t) = \lambda(r) \exp[-t\lambda(r)]$ , where the pulse rate  $\lambda(r)$  is only a function of the distance  $r$  in cluster coordinates. If clusters diffuse adiabatically, a unit at a fixed position on the lattice samples many IEI distributions of varying  $\lambda(r)$  as the clusters move. Assuming ergodicity, the IEI distribution in the fixed frame of reference is

$$P(t) = \frac{1}{\mu} \int \lambda(r)^2 \exp[-t\lambda(r)] 2\pi r dr. \quad (3)$$

where  $\mu = \int \lambda(r) 2\pi r dr$ .

Depending on the functional form of  $\lambda(r)$ , the IEI distribution for a unit at a *fixed* position will decay as a power law and *not* as an exponential. A Gaussian  $\lambda(r)$  in Eq. (3), for instance, leads to  $P(t) \sim t^{-2}$ . The result of numerical integration of the measured  $\lambda(r)$  (Fig. 3)

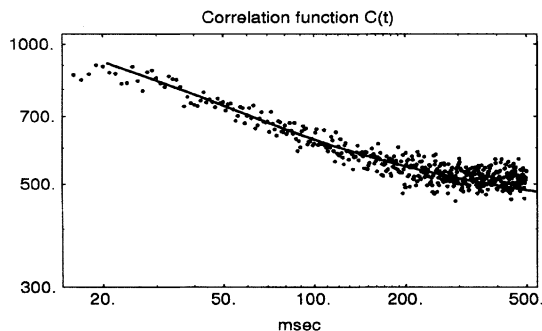


FIG. 4. Measured and predicted (solid line) correlation  $C(t)$  on a log-log scale. The correlation function decays as  $t^{-0.21}$  due to the slow diffusion of activity clusters.

approximates quite well the observed IEI distribution. The power-law range of the IEI distribution is limited by the (nonzero) minimum pulse rate observed in the model. For times  $t > 1/\lambda_{\min} \approx 500$  msec, the IEI distribution  $P(t)$  must decay exponentially.

In the special case of a renewal process, where successive intervals between events are uncorrelated, a power law  $P(t) \sim t^{-\gamma}$  implies  $C(t) \sim t^{\gamma-2}$  ( $1 < \gamma < 2$ ) [17,18]. In our model we find a small but significant deviation from the renewal prediction. While the model's correlation exponent is  $-0.21$ , the renewal exponent should show a faster decay of correlations with an exponent of  $-0.3$ .

Clearly, the scenario of diffusing clusters does not lead to a renewal process. Measuring the serial correlation coefficient reveals that, as in neurophysiological data [18], fast (or slow) intervals are correlated to intervals with the same time scale. Therefore, we need to estimate the correlation directly from the diffusion process:

$$C(t) = C \iint \lambda(r) \lambda(r') G(|\mathbf{r} - \mathbf{r}'|, t) d^2r d^2r', \quad (4)$$

where  $G(r, t)$  is the diffusion Green function and  $C$  is a normalization factor. For times between 10 and 300 msec, the numerically measured diffusion kernel is peaked more strongly near  $r = 0$  than the usual Gaussian. The fit of Eq. (4) is shown in Fig. 4.

The time it typically takes a cluster to diffuse over the intercluster distance sets the time scale for the correlation. Note that the cutoff for  $C(t)$  depends directly on the diffusion constant  $D$ , whereas the cutoff for the IEI distribution is *independent* of the exact speed of diffusing clusters (as long as the assumption of adiabatic diffusion is valid). In the simulation presented in Fig. 1,  $\sqrt{4DT_{\text{cutoff}}} \approx 20$  lattice units, which is the intercluster distance, leading to  $T_{\text{cutoff}} \approx 400$  msec.

The generation of fractal properties by superposition of exponential distributions is a well known concept that was used to explain the  $1/f$  voltage noise spectrum in metals [19]. Continuous random driving also leads to  $1/f$  noise in self-organized criticality models, by tuning the system to a critical state characterized by fractal distribution of avalanches [20]. In contrast to these models, the correlations and temporal cutoffs in our self-organizing model scale not with the system size but with the range of connections. The model's  $1/f^\alpha$  exponent is not universal, since both the exponent and cutoffs depend on the system's parameters (such as the input rate, the degree of inhibition, or the range of local interaction).

The central prediction of the model is that  $1/f$ -type power spectra of neuronal spike trains can be a consequence of the global activity dynamics of the neuronal network. Using the novel technique of optical imaging with fast voltage sensitive dyes [21], Orbach and van Essen [22] report moving elliptical foci of neural activation in response to electrical stimulation.

Unfortunately, experimental limitations do not yet allow the simultaneous recording of single cell spike trains. Therefore, the link between  $1/f$  single-unit power spectra and macroscopic activity dynamics remains, as of now, a conjecture.

Do  $1/f$  signals play an active role in neural computations? The *center-surround* connectivity pattern has been proposed as a computational geometry for various models of auditory, visual, and somatosensory information processing [23,24].  $1/f$  signals may simply be a byproduct of such computations when the neuronal network is pulse coupled. However, to explore the potential role of  $1/f$  signals in computation, we tested the model's response characteristics to more "realistic signals" than white noise by using localized input modulations, which were applied transiently in addition to the previous background input. We find that the network strongly amplifies even small amplitude modulations, since the activity pattern rearranges itself in relation to the stimuli. The decay of the response is much slower than the onset.

Comparing parameter regimes, we find that the  $1/f$  regime accomplishes a tradeoff: In this regime, the perceptual system is sensitive to and amplifies small fluctuations; at the same time, the system preserves a memory of past stimuli in the long time correlation tails. In contrast, as shown in Fig. 5, very fluid activity patterns have a fast and strong amplification response but no memory, while the opposite is true for very rigid activity patterns. The memory inherent in the  $1/f$  system can be used to achieve a "priming" effect: the succession of two stimuli separated by 50–100 msec at the same location results in a stronger response to the second stimulus. Using  $1/f$  for neural computation is an intriguing and promising possibility deserving further research.

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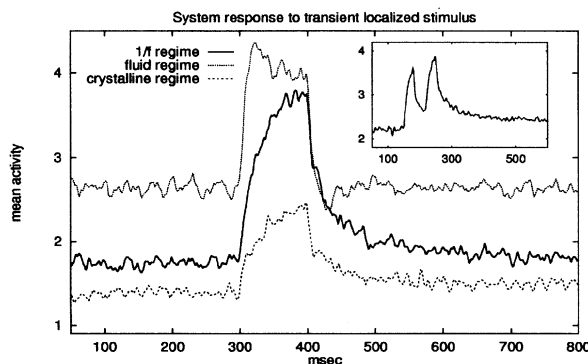


FIG. 5. The stimulus consists of raising the external input rate by 12% of over a circular region of radius 3. The response shown above is the mean spike count per msec within a region of radius 5, averaged over trials. The three traces represent different strengths of inhibition ( $\beta = 0.5, 0.72, 1$ , respectively). The inset displays the response to two successive stimuli at the same location.

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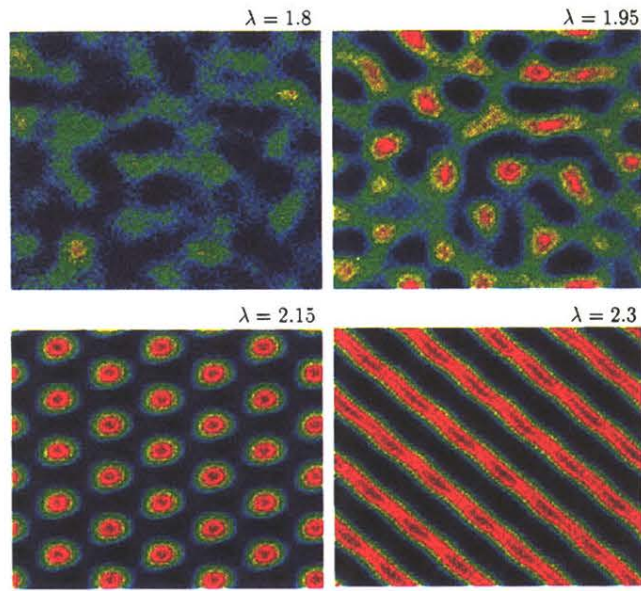


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